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OF THE

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Vol. 50 No. 4

BULLETIN

OF THE

TORREY BOTANICAL CLUB

APRIL, 1923

A study of the embryo sac development and accompanying phenomena in Oenothera rubrinervis

CLAUDE E. O'NEAL

(WITH PLATES 5 AND 6 AND TWO TEXT FIGURES)

Since the announcement by De Vries at the beginning of the present century that *Oenothera Lamarckiana* was giving rise to new species by a process of mutation, the genus *Oenothera* has been subjected to a most thorough examination from almost every angle of botanical science. It has been a special favorite with the plant geneticists, and the morphologists and cytologists have found in its changing species a source of absorbing interest which has been maintained to the present time.

The notable cytological work of Gates (**14**), Lutz (**20**), and Davis (**5**, **6**) on the members of this genus was confined for the most part to the microsporocytes and root-tips of the species studied. The last mentioned, however, as well as Geerts (**15**) and, more recently, Ishikawa (**17**), touched upon the reduction divisions of the megaspore mother cells. As has been pointed out by Gates in this monograph and in other papers, the technical difficulties encountered in such a study are responsible for our present incomplete knowledge of this phase of the life cycle in the genus *Oenothera*.

The present paper has to do with the development of the embryo sac and attending phenomena of ovule development and fertilization in *Oenothera rubrinervis*. The first study of the embryo sac in *Oenothera* was made by Hofmeister (**16**) almost three quarters of a century ago. One of his figures shows the course of the branched pollen tube through the thick nucellar

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structure and its entrance into the embryo sac. He stated that the embryo sac contained from two to four nuclei. He figured this condition for *Godetia*. About three decades after the appearance of Hofmeister's work Kny (**18**) published in his series of charts a description of the earlier phases of the development of the ovule in *Oenotheria biennis*. In 1908, Geerts (**15**) reported the absence of the antipodal cells and one polar nucleus in *Oenothera Lamarckiana;* and, in 1909, Modilewski (**21**) found the same condition in *Oenothera biennis, Circaea lutetiana*, and two species of *Epilobium*. This writer concluded that the tetranucleate embryo sac was a characteristic of the entire family. In 1914, Renner (**24**), working with *Oe. biennis, Oe. Lamarckiana, Oe. muricata* and various hybrids produced by crossing these species, confirmed the findings of Geerts and Modilewski and described fertilization and the early development of the embryo. The report of the tetra nucleate condition of the embryo sac received further confirmation in the same year by the work of Werner (**29**) upon *Oe. Lamarckiana, Oe. biennis, Oe, rhizocarpa, Oe. tetraptera*, and *Oe. coccinea*, as well as upon certain other members of the Onagraceae. The most recent work upon the embryo sac of *Oenothera* is that of Ishikawa* (**17**), who in 1918 published an exhaustive report of his study of this structure, as well as of the phenomena of fertilization in *Oe. nutans* and *Oe. pycnocarpa* (the *Oe. biennis* of the older literature).

OENOTHERA RUBRINERVIS

Oenothera rubrinervis was first described by De Vries (**27**), who found the plant appearing in sowings of *Oe. Lamarckiana*. Its presence was first noted by him in 1889. Before 1901 he had recorded its appearance 66 times as a mutant from *Oe. Lamarckiana*. Gates (**12**) mentions the fact that *rubrinervis*-like plants have been found growing wild in Newfoundland, as well as in western Colorado (**13**) and New Mexico. At first, De Vries considered *Oe. rubrinervis* a "fixed" species, but recently (**28**) he has called it a "half mutant." He thinks that it has been produced "by the copulation of a mutated gamete with a normal *velutina* gamete of *O. Lamarckiana*." In the same publication he showed that *Oe. deserens* is arising from his strain of *Oe.*

* Ishikawa (**17**) and Gates (**12**) give extended bibliographies, which may be consulted for a general summary of the literature upon the genus *Oenothera*.

rubrinervis at the rate of about one to five. Gates (**13**) states that *Oe. rubricalyx* has arisen from *Oe. rubrinervis* by a mutation that is fundamentally chemical in its nature. He states that the difference between the two forms is chiefly one of amount of anthocyanin produced. Shull (**25**) attacked this position and showed by experimental evidence that it was erroneous. The plants with which the latter worked, however, were of uncertain ancestry and Gates insisted that they were hybrids. Lutz (**20**), who has made a cytological study of the species, makes a chromosomal distinction between the Amsterdam plant and the representatives found in Indiana. Davis (**8**) and others have stoutly maintained the hybrid origin of *Oe. Lamarckiana* itself. Davis (**4**) has been able to produce a plant resembling the small-flowered form of *Oe. Lamarckiana* by crossing *Oe. fransciscana* and the Dutch *Oe. biennis*. In his most recent paper on the subject (**8**), this writer states that *Oe. Lamarckiana* arose as a hybrid somewhere in Europe about the middle of the last century. In an earlier publication (**7**) he stated that "with but little doubt, it has come down to us, possibly greatly modified, from certain plants placed upon the market by the seedsmen Carter and Company, of London, about 1860." Gates (**13**) is inclined to accept the hybrid origin of *Oe. Lamarckiana* but is of the opinion that there is no evidence for thinking that its germinal instability has arisen from a single cross. De Vries originally assumed that *Oe. Lamarckiana* was a native American species. Leveillé (**19**),* in a publication which the writer has been unable to secure, states that *Oe. rubrinervis* reverts to *Oe. biennis*. As described by De Vries, the plants when young have leaves with red veins, stems with poorly developed bast fibers, and flowers with "stripes of red of varying width upon the sepals." Lutz (**20**) asserts that the Amsterdam plants have a tendency to produce flowers with crinkled edges, while the Indiana plants usually produce flowers with smooth edges.

The plants from which the material for this study was taken were grown from seed from an *Oe. rubrinervis* mutant that appeared in a sowing of *Oe. Lamarckiana* seed sent to Professor D. M. Mottier by De Vries in 1913. Pollination has been guarded,

* Monographie du genre *Oenothera*. Le Mans. 1908. Review by S. B. Parish in Plant World **13**: 66–72.

and Professor Mottier has had the progeny under observation for nine generations. During this time the plants have been constant for the characters pointed out by De Vries. During the last two seasons, summers of 1920 and 1921, the writer has made a careful examination of the leaf forms in search of the *deserens* type, but no individuals have been found with unusually broad leaves. There is considerable variation in the time of flowering,

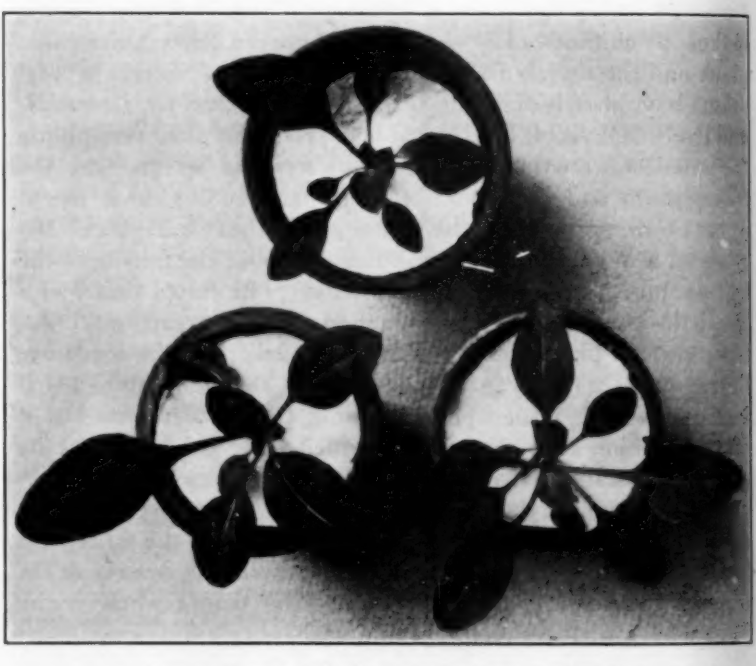

FIG. 1. Young seedlings of *Oenothera rubrinervis*.

as well as a slight color difference in the flowers, but certainly no more than is to be expected in the range of a single species. Our blossoms show the crinkled edges described by Lutz (20) for the Amsterdam plant. This character varies considerably with the individual plants and seems to be influenced by various climatic conditions.

The plants used in this study were grown from seeds sown in a box in the greenhouse in January. When the seedlings

became more or less crowded they were set out in small pots and, after several transferals, they were transplanted about May 1 in the university garden, where they were staked to prevent breakage by the wind and given the usual cultivation. TEXT FIG. 1 shows three of our young plants with their usually shaped leaves.

Treatment of material.—The ovaries in various stages of development were partly stripped of their outer wall and dropped into the chromo-osmo-acetic solution. After two or three hours, they were transferred to a solution lacking the osmic acid, as recommended by Davis (**5**) for *Oenothera* material. For the younger stages of the development of the ovule, this treatment gives excellent results, but for the older stages, after the nucellus has become extensively developed, it is not so satisfactory. At this time the sporogenous cells are so deeply imbedded in the nucellar tissue that fixation is very difficult. For this part of the study a number of killing and fixing agents were tried out. The chromo-osmo-acetic mentioned above, Carnoy's fluid, corrosive sublimate acetic solution, and Bouin's fluid. Bouin's fluid, recommended by Gates (**10**) and used by Ishikawa (**17**), was found to give the best results and was used in securing all stages after the megaspore tetrad was formed.

After the usual method of dehydration and imbedding, sections 4–20 μ in thickness, depending upon the stage of development, were made and stained with anilin-safranin and gentian violet followed by orange G in clove oil. In all, 204 ovaries were cut and examined in sections. Considerable confidence is felt in the statements of development and attending conditions that are given below.

The ovule.—The ovule of *Oenothera rubrinervis* is of the usual anatropous type and is borne on the end of a short funiculus. One ovary was found in which the ovule-stalks were forked and bore two ovules. This abnormality may be added to the long list already noted by Gates (**9**) and others for the genus. At the time of fertilization the ovule is possessed of an outer integument composed of about four layers of cells and an inner one of from one to three layers. The integuments at this time entirely surround the large nucellus in which the embryo sac is deeply imbedded. The arrangement of the parts of the

ovule at the time of fertilization is shown in TEXT FIG. 2. Placentation is central.

Early development of the ovule.—The anlage of the ovule is first noticed as a slight bulge or swelling on the wall of the loculus as shown in PLATE 5, FIG. 1. FIG. 2 shows a stage slightly more advanced, in which the hump is a little more pronounced. There is no evidence of cell differentiation at this time. FIG. 3, of a still later stage, shows a section of an ovule shortly before the appearance of the inner integument initials. FIG. 4 shows the initial development of the inner integument. In the same section the large hypodermal cell which functions as an archesporium may be observed. The occurrence of this cell in the development of ovules seems to have been noted first by Strasburger (**26**) in a plant which he did not name. It was found later by Mottier (**22**), who gave the former credit for first reporting it. Kny (**18**), in his series of charts that has been used extensively in college courses of botany, does not show this cell for *Oe. biennis*, but since the time of this publication, the cell has been observed repeatedly in other genera and Geerts (**15**) described it for *Oe. Lamarckiana*. FIG. 5 is of a section in which two hypodermal cells may be seen lying side by side. Such a condition will result in the formation of two embryo sacs lying side by side, as found by Ishikawa (**17**) in *Oe. pycnocarpa* and *Oe. nutans*.

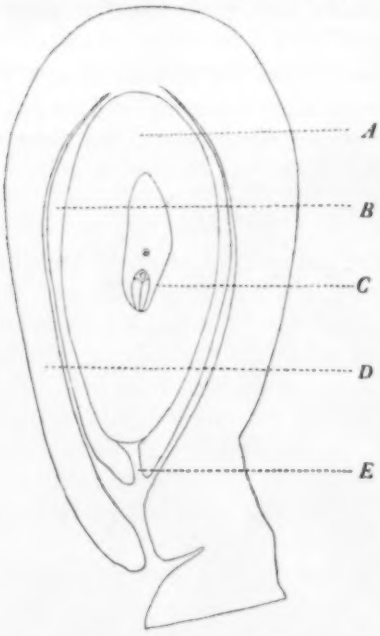

FIG. 2. A camera lucida diagram of the ovule of *Oenothera rubrinervis* showing the deeply imbedded embryo sac, C; the nucellus, A; the inner integument, B; the outer integument, D; and the micropyle, E.

The archesporial cell soon divides in a plane at right angles to its long axis into an outer cell that functions as a tapetum initial and an inner one that becomes the primary sporogenous, or megaspore mother cell, FIG. 6. Shortly after the division of the archesporial cell the initial development of the outer integument may be observed. FIG. 7 shows a section of an ovule in which the development of the outer integument is fairly well advanced.

As shown in FIGS. 1–6 the young ovule very early in its development appears bent upon its growing stalk. This curvature becomes accentuated as the integuments arise. As pointed out above, the inner integument begins as a single encircling row of cells that may be recognized by their larger size and location as well as by their subsequent behavior; the outer integument arises in a similar manner with the exception that, as shown in FIG. 7, the initial ring at first is not closed on the side next to the funiculus. FIG. 8 shows the ovule at the time that the integuments have just reached the end of the nucellus. In this ovule the outer integument completely surrounds the inner envelope of the nucellus. The megaspore mother cell with its large nucellus and dense cytoplasm is very prominent at this time and the developing tapetum, composed in this section of a row of three cells, may be made out also. In FIG. 9 a nucellus containing the large megaspore mother cell and a row of six tapetal cells is shown.

Development of the megaspore.—As shown in the figures, the large elongate megaspore mother cell is deeply imbedded in the nucellus. In some instances, when it begins to divide, a dozen cells may be counted in the tapetal row. The cell has pointed ends and a large nucleus. The cells at hand do not show the resting linin-chromatin reticulum well. While no consistent attempt was made to secure a complete set of mitotic figures in the division of this cell, practically all of those usually described have been found, and some of them, including that of synapsis shown in FIG. 10, were observed repeatedly. This condition in part at least may be due to faulty fixation. The chromosomes are usually in the form of short rods and look quite similar to those recently described by the writer (**23**) for *Datura*. They have been adequately described for this plant by Gates (**14**) in his study of the reduction division of the

microsporocytes. The reduced number seems to be seven, as has been reported by other writers; at least, no more than this number could be found. The diminutive chromosome reported by Lutz (**20**) for the Amsterdam plant was not found in the material studied. FIG. 11 shows a reconstruction stage in which the chromosomes, connecting fibers, and anastomosing strands of cytoplasm stand out with particular clearness. FIG. 12 shows a little later stage in which the cell wall of the first division has been laid down. FIG. 13 shows a stage in the second division similar to that of the first division shown in FIG. 11. The four potential megaspores are shown in FIG. 14. Shortly after the formation of the megaspore tetrad one of the four cells begins the development of the megaspore. The cell nearest the micropyle is usually the functional one but, in some cases, the one at the opposite end of the row develops. This is the reverse of the condition found by Davis (**6**) in *Oe. biennis*. Geerts (**15**) reported that in *Oe. Lamarckiana* the cell nearest the micropyle is always the functional one of the tetrad. Ishikawa (**17**) found that in *Oe. pycnocarpa* and *Oe. nutans* the cell at one end of the row is just as likely to develop as the one at the other, and that either of the two intervening cells may develop, while in certain cases two of the cells in a tetrad may develop simultaneously. In *Oe. rubrinervis* the development of the cell towards the micropyle places the megaspore nearer the center of the nucellus. PLATE 6, FIG. 15, shows the condition of the ovule at the time the megasgore is being developed. The tapetum in this section is composed of eight cells which are still in the meristematic condition. Some sections show a greater amount of tapetal tissue than the one represented in the drawing. The figure does not show the outer integument.

Early in the development of the megaspore the nucleus migrates to the end of the cell next to the micropyle and a conspicuous vacuole appears. The nucleus remains in this position and the vacuole persists until the megaspore is mature. FIG. 16 shows a developing megaspore as well as the three disintegrating sister cells.

Germination of the megaspore.—FIG. 17 shows a longitudinal section of a mature megaspore in which the large nucleus and the central vacuole stand out prominently. This vacuole which appeared in the development of the megaspore is present

until the embryo sac is matured. FIG. 18 shows the bi-nucleate stage of the embryo sac. This section is cut in such a way that the vacuole does not show, but a study of the adjoining sections reveals its presence. This stage of development follows shortly after that shown in FIG. 17, and the nuclei here shown divide almost immediately without changing position. This results in the tetra-nucleate condition shown in FIG. 19. Shortly after the formation of the four nuclei, plasma membranes appear around the cytoplasmic masses containing three of them and the usual egg apparatus with its two synergids and egg cell is formed, as shown in FIG. 20. The fourth nucleus usually draws away from the egg apparatus. While these changes have been taking place strands of cytoplasm have appeared in the vacuole, as is represented in the mature embryo sac given in the figure.

Coulter and Chamberlain (3) listed *Oenothera* in the group of plants having ephemeral antipodals. The present writer at the outset, knowing what an easy thing it would be to overlook the fragments of these cells, had the feeling that this was likely the condition. Literally thousands of sections have been examined for evidence supporting this view, but as stated above, the megaspore nucleus divides but twice, so the antipodals and one polar nucleus are completely lacking. This finding for *Oe. rubrinervis* is in keeping with that of Geerts (15) for *Oe. Lamarckiana*; Modilewski (26) and Ishikawa (17) for *Oe. biennis*; Renner (24) for *Oe. biennis*, *Oe. Lamarckiana*, *Oe. muricata*, and various hybrids produced by crossing these species; and Werner (29) for *Oe. Lamarckiana*, *Oe. biennis*, *Oe. rhizocarpa*, *Oe. tetraptera*, and *Oe. coccinea*.

The tetra-nucleate embryo sac.—The tetra-nucleate embryo sac has been reported for about sixty species of plants. Over half of these are from the order Myrtales, to which the Onagraceae belong. The tendency to this condition seems rather wide spread in the Archichlamydae and is found in the Orchidales and Liliales of the monocotyledonous group. Doubtlessly, the development of the tetra-nucleate embryo sac is but one expression of the tendency to eliminate the divisions that occur after the reduction division of the mother cell. A few cases have been reported from the Primulales, a lower order of the Metachlamydae; but, as has been pointed out by Coulter (2), it is doubtful if this tendency is a very strong one in this group.

Many of the orders in which the plants with four-nucleate embryo sacs are found have also species in which the antipodals are ephemeral. It is not clear how the latter condition could have given rise to the former. In the Myrtales, as well as in other orders in which the tetra-nucleate embryo sac has been reported, sacs with sixteen nuclei have been found. If there is a genetical relationship between these three conditions, it must be looked for in smaller groups. Ishikawa (17) says that the tetra-and sixteen-nucleate embryo sacs are to be regarded as representing a derived type, "probably caused by mutation and variation in certain stages of phylogenetic development." At the present stage of our knowledge this is probably as accurate a statement of the condition as it is possible for us to make.

Fertilization.—The ripe pollen grain as described by Geerts (15) for *Oe. Lamarckiana* has a generative cell and a tube cell. The division of the generative cell to form the sperms was not observed but it evidently occurs in the pollen tube. Sections were found showing the sperms and the tube nucleus in the tube. In most cases they are obscured by the large amount of starch present in the tube. In a pollen tube, the tip of which had just reached the embryo sac, the sperms and vegetative nucleus were observed in the part of the tube in the micropyle. Ishikawa (17) found that three sperms were formed in *Oe. pycnocarpa* and *Oe. nutans*. There are but two developed in *Oe. rubrinervis*. The sperms seem to enter the egg apparatus through a synergid as described by Ishikawa, but the material at hand does not show enough cases to be positively confirmatory on this point. The flowers from which the material for this paper were taken were guarded and at the proper time hand pollinated. It was found that with midsummer temperatures the pollen tubes were able to reach the embryo sac in about thirty-six hours after pollination and that fertilization (FIGS. 21, 22) occurred soon afterwards. In practice large masses of pollen were placed upon the stigmas. The large number of pollen tubes developed disrupted the inner tissue of the style to such a degree that the extent of their course could be made out by examining the styles with a binocular. But comparatively few of the tubes reached the micropyles. Numerous theories have been given for such failures. One mentioned by Compton (1) and based upon the supposed analogy between fertilization and infection in animals

seems so unlikely as to warrant comment, even though out of the scope of this paper. According to this theory, the pollen tubes act as *antigens* and stimulate the formation of specific antibodies by the cells of the pistil. The outstanding objections to this belief are: (1) that there is no complete circulation in plants as in animals, so that but comparatively few cells could be stimulated, and (2) that the time between pollination and fertilization is too short for the development of anti-substances in sufficient quantities to produce such a striking effect, even if the circulation in plants were in all ways the same as in the higher animals.

Ishikawa (**17**) found that fertilization was double in *Oe. pycnocarpa* and *Oe. nutans* and Modilewski (**21**) reported it as probably double in *Oe. biennis*. The writer has been unable to confirm this finding in *Oe. rubrinervis* and has the feeling that it does not occur in this plant. The chromosomes were not counted in the endosperm and the whole point requires further investigation. It is needless to state that the *Oenotherae* do not furnish ideal material for fertilization studies.

SUMMARY

1. The ovules of *Oenothera rubrinervis* arise in the usual fashion from a slight swelling that appears upon the wall of the ovary.

2. Early in the development of the ovule an archesporial cell is differentiated that soon divides into an outer tapetal initial and an inner primary sporogenous cell.

3. The tapetum initial gives rise to a tapetal row of about a dozen cells, and the primary sporogenous cell develops into the usual potential megaspore tetrad.

4. The cell of the tetrad nearest the micropyle usually becomes the functional megaspore, although in some cases the one at the opposite end of the row may develop.

5. Early in the development of the megaspore, a large central vacuole appears which persists until after the embryo sac development is completed.

6. Upon germination the nucleus of the megaspore divides but twice, so that the mature embryo sac contains but four nuclei instead of the usual eight.

7. Fertilization occurs in about thirty-six hours after pollination and is probably single.

In conclusion, the writer is pleased to take the opportunity of acknowledging his debt of gratitude to Professor D. M. Mottier, of Indiana University, who assigned this problem and who, by friendly advice and encouragement, has aided much in bringing this paper to its present stage of completion.

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Explanation of plates 5 and 6

PLATE 5

FIG. 1. The anlage of the ovule before cell differentiation has begun, × 350.

FIG. 2. A slightly later stage, × 350.

FIG. 3. The young ovule shortly before the appearance of the inner integument initials, × 350.

FIG. 4. A young ovule in which the primordial cell and the inner integument initials are shown, × 350.

FIG. 5. A stage similar to that shown in FIG. 4, in which two primordial cells may be seen lying side by side, × 350.

FIG. 6. A slightly later stage in which the tapetal initial and the primary sporogenous cells resulting from the division of the primordial cell are shown, × 350.

FIG. 7. An early stage in the development of the outer integument, × 350.

FIG. 8. A young ovule showing the large megaspore mother cell, nucellus with the developing tapetum, and the inner and outer integuments, × 200.

FIG. 9. The nucellus of a latter stage in which a megaspore mother cell and a row of six tapetal cells are shown, × 350.

FIG. 10. A megaspore mother cell in the synaptic condition, × 740.

FIG. 11. A megaspore mother cell in the late telophase of the first division, × 740.

FIG. 12. The two daughter cells resulting from the first division of the megaspore mother cell, × 740.

FIG. 13. A late telophase of the second division of the second division of the megaspore mother cell, × 740.

FIG. 14. A megaspore tetrad, × 740.

PLATE 6

FIG. 15. A nucellus surrounded by the inner integument and containing the developing megaspore and a tapetum of eight cells which are still in the meristematic condition, × 200.

FIG. 16. The young megaspore, with its large nucleus and central vacuole, and the three disintegrating cells, × 740.

FIG. 17. A mature megaspore, × 740.

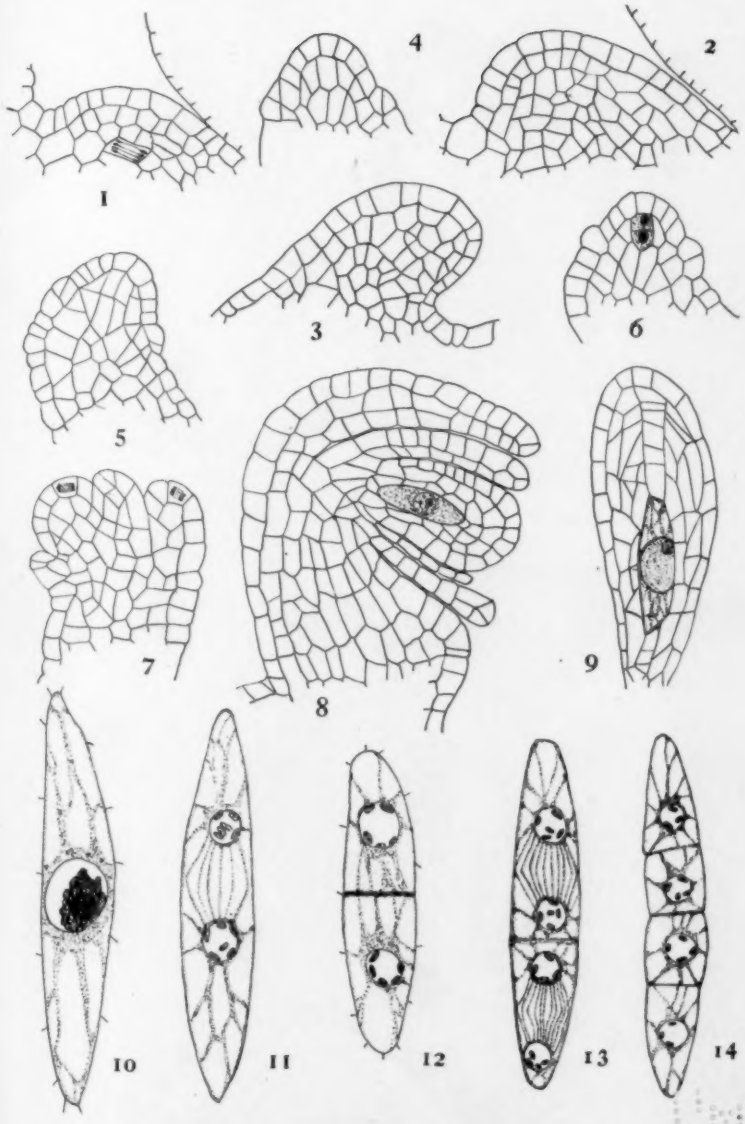
FIG. 18. A binucleate stage of the embryo sac, × 740.

FIG. 19. A developing embryo sac with four free nuclei, × 740.

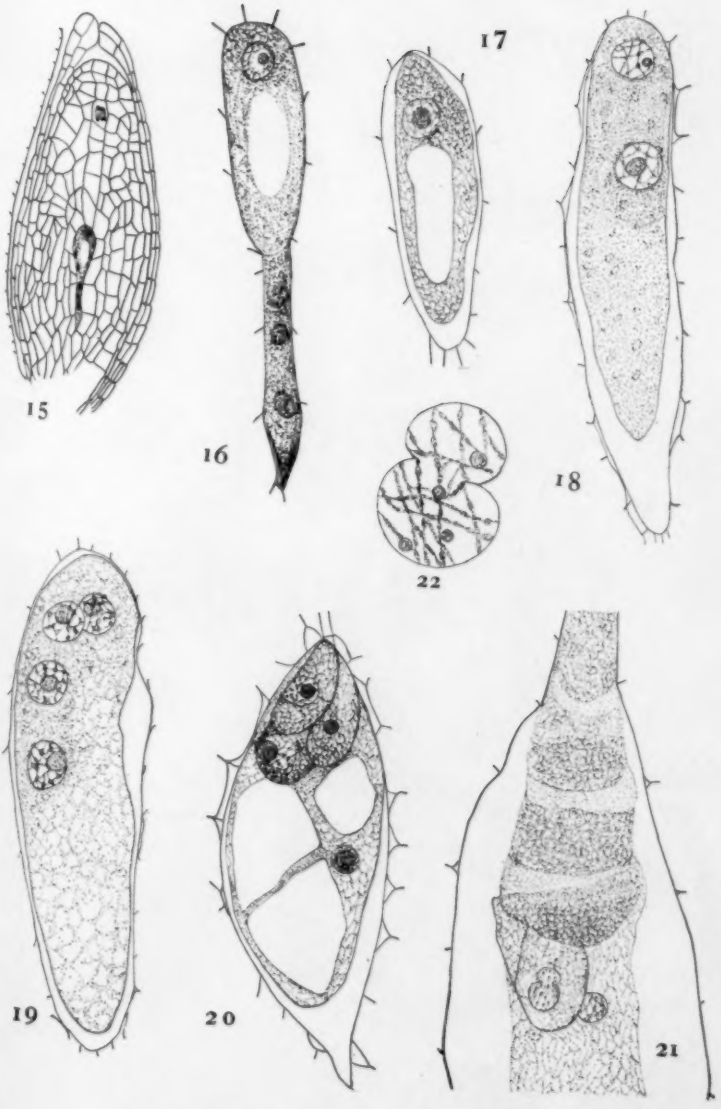
FIG. 20. A mature tetra-nucleate embryo sac, × 740.

FIG. 21. A fertilization stage, × 1200.

FIG. 22. A fusion of the (larger) egg cell nucleus and the nucleus of the sperm (somewhat idealized), × 1800.



O'NEAL: OENOTHERA RUBRINERVIS



O'NEAL: OENOTHERA RUBRINERVIS

Windsorina, a new genus of Rapateaceae

HENRY ALLAN GLEASON

(WITH PLATE 7)

The small family Rapateaceae is still one of the most poorly known groups of South American plants. Seubert knew but three genera and six species when he monographed the group for the Flora Brasiliensis in 1847. At approximately the same period the Schomburgk brothers were exploring British Guiana actively and brought out other remarkable species from the dense forests of that region, and Spruce contributed still other novelties from northern Brazil and southern Venezuela. Körnicke summarized the existing knowledge of the family in 1873, and his treatment remains the latest monograph. The greatly condensed discussion given the family by Engler in 1888 indicates that it was still scantily represented in continental herbaria, although Bentham and Hooker seem to have had fairly abundant material at hand when they published Genera Plantarum in 1883. It is still poorly illustrated in American herbaria, because of lack of recent exploration in the hinterland of the Guianas and Brazil, although the recent collections of Hitchcock, Gleason, and De La Cruz have included several of the coastal species.

The characters and history of the family were published in detail by Körnicke and need no re-statement. The distinction of genera lies chiefly in the structure of the anthers and the nature of the inflorescence. The latter is invariably a head or a headlike umbel, is usually subtended by an involucre of one or two foliaceous bracts, and is borne on a long peduncle arising from the base of a leaf and protruding from within the leaf-sheath.

On June 27, 1921, the writer was walking through the six miles of dense tropical forest between Kangaruma and Potaro Landing, on the Potaro River, British Guiana. His attention was attracted by a gregarious plant with broadly linear leaves, growing in a small marsh along the trail and apparently sterile. Closer examination showed that each plant bore numerous long

peduncles, arising in fascicles from one or more of the leaf-sheaths and terminating in a subcapitate cluster of bracted flowers. Subsequent examination and comparison with the material at the New York Botanical Garden demonstrated beyond a doubt that the plant was a member of the Rapateaceae and that it could not be assigned to any of the seven genera hitherto recognized.

WINDSORINA gen. nov.

Herba glabra paludosa Rapateacearum; pedunculi axillares fastigiati 3–9; inflorescentia terminalis subumbellata sine involucro; flores pedicellati circa 10–20 ovoidei bracteis imbricatis 9–12 suffulti; calyx erectus, sepalis 3 convolutis; petala 3 libera limbo ovato flavo; stamina 6, filamentis liberis ante anthesin brevibus post anthesin contortis, antheris quadrilocularibus lineari-lanceolatis poro obliquo subterminali apertis; capsula ovoideo-prismatica loculicida trilocularis, seminibus in loculo solitariis subglobosis albis dorso maculatis ad apicem cartilagine appendiculatis.

Windsorina guianensis sp. nov.

Herba 1 m. alta gregaria; foliorum vagina lineari, lamina late lineari multinervia venosa; pedunculis longis erectis angulato-compressis angustis sursum sensim clavatis; pedicellis 5–15 mm. longis; bracteis inferioribus lanceolatis acuminatis, mediis ovatis acutis, superioribus oblongo-obovatis; sepalis lanceolatis erectis post anthesin clausis; petalorum limbis ovatis; filamentis planis; capsula straminea; seminibus minute rugulosis.

The type is *Gleason 272*, deposited in the herbarium of the New York Botanical Garden.

Since Schomburgk named a genus, *Saxo-Fridericia*, and a species, *Rapatea Friderici-Augusti*, in honor of a contemporary German ruler, the present generic name *Windsorina* is given in commemoration of the House of Windsor of Great Britain.

Windsorina guianensis is essentially acaulescent, as are all other members of the family, bearing several erect or ascending leaves which reach a height of a meter. Of this length, the lower fifth or fourth is flattened into a sheath, bearing the midvein on one side and not in the center, and about 25 mm. wide. At the summit of the sheath, the leaf contracts to 10 mm. wide, and then expands into the broadly linear, acuminate blade, which is 50–75 mm. wide. As in all Rapateaceae, the blade bears a peculiar relation to the sheath. The midvein of

the latter is prolonged into the midvein of the blade, the back of the sheath becomes the margin at the point of constriction and is thence continued as one margin of the blade, which is itself slightly inequilateral. The blade contains numerous longitudinal ribs, arising from the midvein, running almost parallel to it, and connected by numerous transverse veinlets.

From the axils of some of the leaves arise clusters of three to nine erect peduncles as much as 6 dm. long, more or less fastigiate at the base, and subtended by a few narrowly lanceolate, colorless, scarious, one-nerved, acuminate scales 30–55 mm. long. Other members of the family have normally solitary peduncles, although Körnicke mentions that two may sometimes occur. They are strongly angled, at least when dry, and double or treble their diameter toward the apex. The inflorescence proper is a capitate umbel, bearing ten to twenty flowers. The lowest of these is not subtended by a bract, and is borne on the longest pedicel, which may be 12 mm. long and appears almost as a continuation of the stem. On the opposite side of the umbel is a scarious, ovate-lanceolate, acute bract 10–15 mm. long. When the lowest flower and lowest bract are removed, a second bractless flower is discovered, situated opposite a second bract. Each of the remaining flowers in turn is on a shorter pedicel, until the central flowers of each umbel are almost sessile, and the respective bracts also decrease regularly in size. In the bracteal characters, *Windsorina guianensis* differs from other members of the family. Two bracts only occur in five of the genera: in three genera these are separate, in *Rapatea* they are barely connate at base, and in the little-known *Saxo-Fridericia* they are connate throughout into an enclosed cone surrounding the flowers and broken by them at or before anthesis. In one genus, *Spathanthus*, there is a single bract, which is adnate to the axis of the spicate inflorescence and closely simulates the spathe of an aroid. In *Stegolepis* the involucre is completely lacking. If the bracts of *Windsorina* are regarded as appertaining to each flower, and not as constituting an involucre to the whole umbel, differences from the other genera are again apparent, for such bracts have been observed, according to Körnicke, only in *Rapatea*, in which the true involucre is particularly well developed. In the pedicelled flowers, *Windsorina* agrees only with *Rapatea*.

The flowers become 7–8 mm. long at maturity and are subtended and almost enclosed by nine to twelve smooth brownish-yellow bracts. Of these, the lowest is the smallest and is long-acuminate into a slender subulate tip; the second is abruptly acuminate into a short tip, while the upper ones are obtuse or barely acute and somewhat thickened at the apex. Their shape also changes progressively, the outer being lanceolate, the middle elliptic, and the innermost oblong-obovate. Their size ranges from 3 to 5 mm. long by 1–2 mm. wide.

When the bracts have been removed one by one, the three sepals are finally exposed. They are similar to the bracts in color and texture, ovate-lanceolate, acute, 5–6 mm. long, 2 mm. wide, and closely rolled together after anthesis.

Körnicke noted the great rarity of expanded corollas in all the dried material of this family. Among the scores or even hundreds of growing plants of *Spathanthus unilateralis* and *Rapatea paludosa* observed by the writer in British Guiana, only one exhibited an open corolla, and on fifty or more fertile plants of *Windsorina* not one open corolla was noted. It is probable that the family in general is characterized by a short period of anthesis, the petals expanding quickly, remaining open for a short time only, and then wilting and contracting back into the calyx. Dissections of unopened buds show three yellow triangular-ovate petals with basal colorless claws, the whole about equaling the sepals. After anthesis, the claw is found to be considerably longer and the limb is recurved, more or less contorted, and faded to brown. Unopened stamens have short, colorless, flat, ovate-oblong filaments less than 1 mm. long, which after anthesis are 5–6 mm. long and greatly contorted into several folds or loops. The anthers are yellow, lanceolate in outline, about 3 mm. long, and quadrilocular, the two inner loculi extending only about three-fifths of the distance to the apex, above which point the anther is conspicuously narrower. It opens by a small pore on the inner surface just below the apex. This becomes visible only after anthesis, when the whole anther is shriveled and the empty pollen-sacs bright reddish brown.

The structure of the anthers is of considerable taxonomic importance in the Rapateaceae. In *Cephalostemon* and *Saxo-Fridericia* they open by a terminal longitudinal cleft, in *Schoeno-*

cephalium by two terminal pores, in *Rapatea* by a pore in a terminal appendage, in the remaining four by a single oblique terminal pore. Among these four, *Windsorina* is distinguished by its pedicelled flowers on fastigiate peduncles, its lack of a true involucre, as well as characters of the fruit.

The ovary is broadly ovoid or subglobose, truncate at the apex, white in color, and with three rounded lobes. The style is slender and about 3.5 mm. long. The fruit is a broadly ovoid-prismatic, loculicidal, three-celled, yellow capsule, not exceeding the subtending calyx in length. Each valve is thin and scarious at the base but stiff and coriaceous above, ovate-rhombic in shape, and with a broad rounded notch at the apex. There is a single ovule in each cavity. The ripe seed is nearly globose, but somewhat flattened on the inner surface. On the outer surface, the chalaza is indicated by an oval brown spot near the apex, above which the seed bears a flattened, narrowly triangular, brownish-yellow appendage nearly 1 mm. long. The testa is white, shining, and minutely rugose. In the characters of the fruit *Windsorina* agrees with *Monotrema*, *Rapatea*, and *Cephalostemon*; in *Spathanthus* the fruit is unilocular by abortion, and in the other three genera the ovules are two or more in each loculus.

The eight genera may be separated as follows:

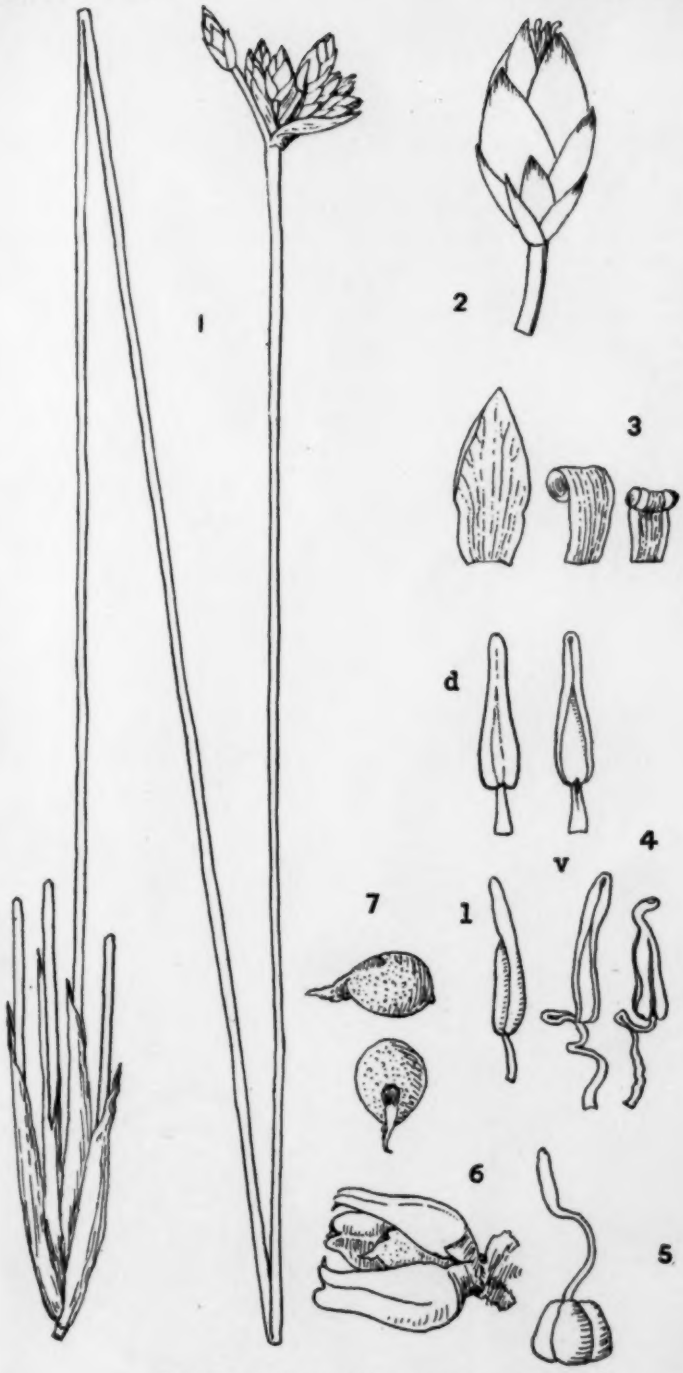
Flowers pedicelled.	
Peduncles numerous; involucre none	*Windsorina.*
Peduncles solitary; involucre of two bracts	*Rapatea.*
Flowers sessile.	
Involucre none	*Stegolepis.*
Involucre of a single bract, spathe-like	*Spathanthus.*
Involucre of two bracts united into a hollow cone	*Saxo-Fridericia.*
Involucre of two free bracts.	
Anthers opening by a terminal slit	*Cephalostemon.*
Anthers opening by a terminal pore	*Monotrema.*
Anthers opening by two terminal pores	*Schoenocephalium.*

NEW YORK BOTANICAL GARDEN

Explanation of plate 7

WINDSORINA GUIANENSIS Gleason

1. Inflorescence, natural size. 2. Single flower, × 4. 3. Petals before and after anthesis, × 5. 4. Stamens before and after anthesis, × 5, *d*, dorsal, *v*, ventral, and *l*, lateral views. 5. Pistil, × 5. 6. Mature fruit, × 6. 7. Seeds, × 6.



WINDSORINA GUIANENSIS GLEASON

INDEX TO AMERICAN BOTANICAL LITERATURE
1921–1922

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to foresty, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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